THE MORPHOLOGY AND RELATIONSHIPS OF *MUELLERENA WATTSII* (HARVEY) SCHMITZ (CERAMIACEAE: RHODOPHYTA)

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Summary

The morphology and life history of *Muellerena wattsii* (Harvey) Schmitz is described and its relationships discussed. It is recognized as belonging to the tribe Crouanieae (Ceramiales, Rhodophyta) on the basis of thallus morphology and stages in development of the procarp and carposporophyte. Features including regularity of branching pattern and elaboration in development of the involucre surrounding the carposporophyte suggest a probably phylogenetically advanced condition.

Introduction

Muellerena wattsii (Harvey) Schmitz in Schmitz & Hauptfleisch was described as *Crouania wattsii* by Harvey (1863), who considered it closely allied to *C. agardhiana* [now *Ptilocladia agardhiana* (Harvey) Wollaston 1968]. Schmitz (1889) listed the species as belonging to a new genus *Muellerella* which, however, he formally described (in Schmitz & Hauptfleisch 1897) as *Muellerena* with *M. wattsii* as the type species.

Muellerena is a monotypic genus seemingly quite distinct from other closely related genera. Schmitz (1889) placed it in the Dasyphileae but Kylin (1956) suggested that it was probably more closely related to *Crouania* and considered it to be insufficiently known for correct placement. Hommersand (1963), after examining specimens of *M. wattsii* in TCD, concluded that it was probably correctly placed in Dasyphileae. However, detailed study of both vegetative and reproductive features show that it is best placed in the Crouanieae.

Material used for investigation has been mainly drift plants collected at Stinky Bay, Nora Creina, S. Aust. (*Wollaston*, 14.xi.1955; ADU, A20004; *Wollaston*, 19.v.1964; ADU, A27924) and at Seal Bay, Kangaroo I., S. Aust. (*Womersley*, 21.i.1965; ADU, A28819). These collections included both tetrasporangial and carposporangial plants.

Muellerena wattsii (Harvey) Schmitz in Schmitz & Hauptfleisch 1897: 496. De Toni 1903: 1388; 1924: 490. Lucas 1909: 50. Lucas & Perrin 1947: 344. Mazza 1911: No. 397.

Crouania wattsii Harvey 1863: synop. No. 637, pl. 291. J. Agardh 1876: 86. Tisdall 1898: 503.

Muellerella wattsii Schmitz 1889: 451 (nomen nudum). Kylin 1956: 397.

Thallus to 13 cm high with terete, sparingly-branched axes bearing alternate, distichous lateral branches up to several cm long and usually pinnately branched in the outer part (Fig. 1); laterals borne from alternate axial cells, occasionally with a shorter branch (less than 1 cm long) opposite or between the longer laterals (Fig. 2). These shorter branches are initiated on the basal cell of an original whorl-branchlet and develop in its place. Axial cells are 1–1½ times as long as broad with cells of the central mature thallus usually 350–400 μm long. Each axial cell bears from its upper part a whorl of 5 whorl-branchlets (Figs. 3ii, 4), with the exception that those cells which bear lateral branches often produce only 3 whorl-branchlets and 1 lateral branch (Fig. 3i, iii).

Growth takes place by transverse divisions of an apical cell and whorl-branchlets are initiated usually on the sub-apical cell (Fig. 5) with the first-formed initial of each whorl in a lateral position, the second and third to the right and left of it respectively and those last-formed opposite the first one (Fig. 3ii). During early development, lateral branches are characteristically curved due to their having the first-formed and hence the longest whorl-branchlets borne on the abaxial (outer) side, while the shortest most immature ones are adaxial in position (Fig. 5). However, after initial elongation of 1–several mm, each young lateral produces at its tip further alternate, distichous

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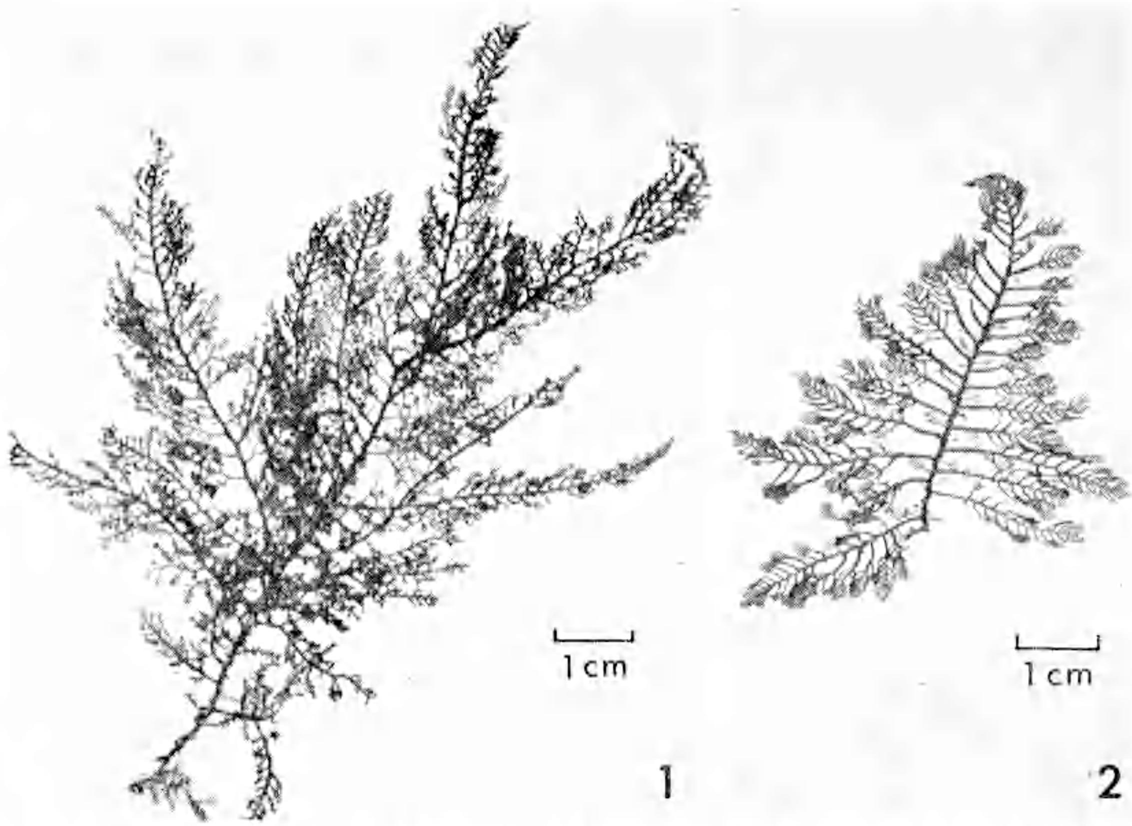


Fig. 1. Plant habit (Stinky Bay, Nora Creina, S. Aust., drift, *Wollaston*, 19.v.1964, ADU A27924).
Fig. 2. Type specimen, TCD (Warrnambool, Vic., cast ashore, *Watts*, Sept. 1860, Harvey 221). Regular, distichous arrangement of short lateral branches and occasional shorter branches opposite or between the longer ones.

lateral branches on alternate axial cells. On each of these axial cells the lateral branch is initiated first followed by whorl-branchlets to the right and left of it and the last formed one opposite the lateral branch (Fig. 3i, iii, iv). Most lateral branches cease growth early but a few continue to elongate and form indeterminate thallus branches (Fig. 2). Young cells enlarge rapidly and gland cells and tetrasporangia may occur very close to branch tips.

Mature whorl-branchlets consist of several consecutive di- or tri-chotomous whorls of cells, and terminate in short, 2- or 3-celled chains of small cells, each up to 7 μm diam., often terminated by a slender, elongate hair to 180 μm long (Fig. 4). Cells of whorl-branchlets are 1–2 times as long as broad and up to 60 μm long in the central part of mature whorl-branchlets. Whorl-branchlets are commonly lost from older axes and particularly from the upper and lower axial face between the distichously-arranged branches.

Axes are corticated, except when very young, by descending, branched filamentous rhizoids of elongate cells which arise from the basal cells of whorl-branchlets (Fig. 6) and intertwine to form a dense axial covering with short, horizontal branches, composed of a chain of several small cells, projecting outwardly. In older parts of the thallus the axial cells become very thin-walled and may be almost indistinguishable within the cortical cylinder.

Ovoid to pyriform gland cells up to 16 μm long, each within a thick gelatinous sheath, occur as homogeneous, refringent structures borne in place of outer branches of whorl-branchlets and scattered, sometimes abundantly, over the thallus (Fig. 7). Cells of the thallus appear to be uninucleate although properly fixed material has not been available for study with specific nuclear stains. Rhodoplasts vary from small and rounded in young cells to reticulate and finally to elongate in mature cells (Fig. 8i–iii).

Procarp and Carposporophyte—Carpogonial branches, 4-celled when mature, are initiated singly on a supporting cell which is one of a whorl of 4 cells borne from the upper part of the terminal cell of a short 2 (-3)-celled special fertile branch (Fig. 9). The fertile branch is produced at the outer end of the basal (or second) cell of a whorl-branchlet and replaces one branch of the normal di- or trichotomy. The sub-apical cell of the fertile branch also bears a whorl of (4-)5 cells (Fig. 9). Each fertile branch is initiated near the tip of a branch axis, so that a succession of maturing procarps and carposporophytes is produced as the branch axis elongates. Cells of the carpogonial branch are formed by transverse divisions of an initial cell which is cut off outwardly from the supporting cell (Figs. 10–13). The lower three cells stain densely and appear homogeneous in structure while the carpogonium is smaller, often with a densely-staining protoplast concentrated in one portion of the cell, and bears an elongate trichogyne, to 90 μm long, usually swollen at its base and its tip (Figs. 12-14). A sterile cell is formed on the upper side of the supporting cell after initiation of the carpogonial branch and is usually well-developed by the time the carpogonial branch is mature (Figs. 11–13).

Following fertilization, the carpogonium enlarges and becomes rounded in form while the trichogyne degenerates and an auxiliary cell develops from the upper part of the supporting cell (Fig. 15). At this stage the three sterile cells, making up the whorl which includes the supporting cell of the carpogonial branch, commence to enlarge and each becomes roughly triangular in shape; the sterile cell borne on the supporting cell divides to form a chain of several cells (Fig. 15) while the cells forming the whorl on the sub-apical axial cell elongate and produce terminally the first cells of branched involucral filaments (Fig. 16). Fusion takes place by means of a connecting cell between the carpogonium and the upper part of the auxiliary cell, leaving only one or two small cell fragments in place of the carpogonium on the degenerating carpogonial branch (Fig. 17).

Branched involucral filaments formed from the enlarged sterile cells on the apical and subapical axial cells of the fertile branch develop rapidly, and loosely surround the developing carposporophyte (Fig. 17). The basal cells of the upper whorl of filaments remain characteristically triangular and larger than other cells of these branches (Fig. 17). The auxiliary cell cuts off a gonimoblast cell from its upper side and simultaneously forms a pit-connection with the apical cell of the fertile branch axis (Fig. 18). Through this connection nutriment is possibly conveyed more directly to the carposporophyte, while the old supporting cell acts as the basal cell of an involucral filament. Gonimolobe initials, which each give rise to a rounded group of carposporangia, develop successively with the first one or two gonimolobes produced in a lateral position. Further gonimolobes are produced without regular order so that a total of 6 or more groups of carposporangia at various stages of development may be present at the one time (Fig. 19). As the first carposporangia mature, the newly formed pit-connection between the axial cell and auxiliary cell gradually widens and the connection between the lower part of the auxiliary cell and the supporting cell remains small and probably non-functional or is finally broken (Fig. 19). The involucral filaments, each branched several times, curve upward and loosely surround the mature carposporophyte.

Spermatangia—not recorded.

Tetrasporangia—Spherical, tetrahedrally-divided tetrasporangia, seldom greater than 25 μm diam., are borne on the outer cells of whorl-branchlets in place of vegetative branches (Fig. 20), in a similar position to gland cells. They may occur on any part of the thallus but are usually most abundant on young branches.

Type Locality—Warrnambool, Vic. (*Watts*, Sept. 1860).

Holotype—TCD, Harvey Alg. Aust. Exs. No. 221.

Distribution—From West I. and Kangaroo I., S. Aust., to Warrnambool, Vic.

Discussion

Muellerena wattsii is characterized by the following vegetative and reproductive features:

(a) a consistent branching pattern and short lateral branches developed regularly from the outer end of axes,

(b) whorl-branchlets in whorls of 5 on each axial cell, except on those which bear short lateral branches,

(c) fusion between the lower part of the auxiliary cell and the fertile axial cell during carposporophyte development,

(d) a distinct filamentous involucre surrounding the carposporophyte and involving the original supporting cell of the carpogonial branch.

Vegetative features such as the alternate-distichous arrangement of short lateral branches at the tip of each previously-formed lateral, the form of axial cortication, and the consistency in arrangement and number of whorl-branchlets on each axial cell, suggest a relationship with the *Ptilocladia* group of the Crouanieae. These features were regarded by Wollaston (1968, p. 404) as indicative of a phylogenetically advanced thallus form. Hommersand (1963) stated that *Muellerena wattsii* was quadriverticillate and he considered the order of initiation of whorl-branchlets in a rhodomelacean sequence (the first abaxial, the next two to the right and left of the first and the fourth one adaxial) to be a significant taxonomic feature characteristic of the Dasyphileae. However, *M. wattsii* has in fact 5 whorl-branchlets per whorl except where short lateral branches are produced, and in these whorls the order of development of the 4 initials could have arisen from a crouanioid sequence in which the second branchlet is formed opposite the first and the third and fourth at right angles to them. Suppression of the adaxial branchlet when adjacent to another axis is commonly found in a number of taxa, for example, in species of *Platythamnion* J. Agardh and *Amoenothamnion* Wollaston (Wollaston 1968). In *Muellerena wattsii* this could explain development of the intermediate whorl-branchlets of each whorl prior to initiation of the adaxial whorl-branchlet(s), which at times is completely lacking at the base of lateral branches. *M. wattsii* clearly evolved a stable pattern of branching and on this basis is probably vegetatively advanced.

Several other vegetative features of *M. wattsii* also suggest relationship with the Crouanieae group. Gland cells, not previously recorded for *M. wattsii*, are similar in form to those found in *Ptilocladia australis* (Harv.) Wollaston, *P. vestita* (Harv.) Wollaston, and *Gulsonia annulata* Harvey, although they lack

Fig. 3. i-iv. Arrangement and sequence of initiation of short lateral branches (L) and whorl-branchlets in whorls on successive axial cells near the tips of axes. (Diagrammatic.) i, ii, iii represent in transverse section the 3 cells shown in iv.

Fig. 4. Transverse section of axial cell bearing a whorl of 5 whorl-branchlets with tetrasporangia.

Fig. 5. Tip of branch axis showing alternate, distichous arrangement of young lateral branches (L_1–L_4) on alternate axial cells and abaxial initiation of first-formed whorl-branchlets on cells of lateral branch axes. (Whorl-branchlets on faces of axes omitted for clarity.)

Fig. 6. Branched, descending cortical rhizoids borne on basal cell (b) of a whorl-branchlet.

Fig. 7. Gland-cells borne in place of branches of whorl-branchlet.

Fig. 8. Rhodoplast structure (i) young cell with rounded rhodoplasts, (ii) enlarging cell with reticulate rhodoplasts, (iii) mature cell with elongate rhodoplasts. (Diagrammatic.)

Fig. 9. Carpogonial branch on special 2-celled fertile branch borne in place of a whorl-branchlet branch on basal (or second) cell of whorl branchlet.

Fig. 10. Carpogonial branch initial cut off outwardly from supporting cell.

Fig. 11. Young carpogonial branch, 3-celled stage, on supporting cell which also bears a small sterile cell (s).

Fig. 12. Carpogonial branch, 4-celled, with developing trochogyne.

Fig. 13. Carpogonial branch with fully elongated trichogyne.

Fig. 14. Fusion of spermatium (sp) with mature trichogyne.

Fig. 15. Auxiliary cell (a) formed from upper side of supporting cell; carpogonial branch with enlarging carpogonium (c) and terminal remnant of trichogyne; sterile cell (s) bearing first cells of involucral filament.

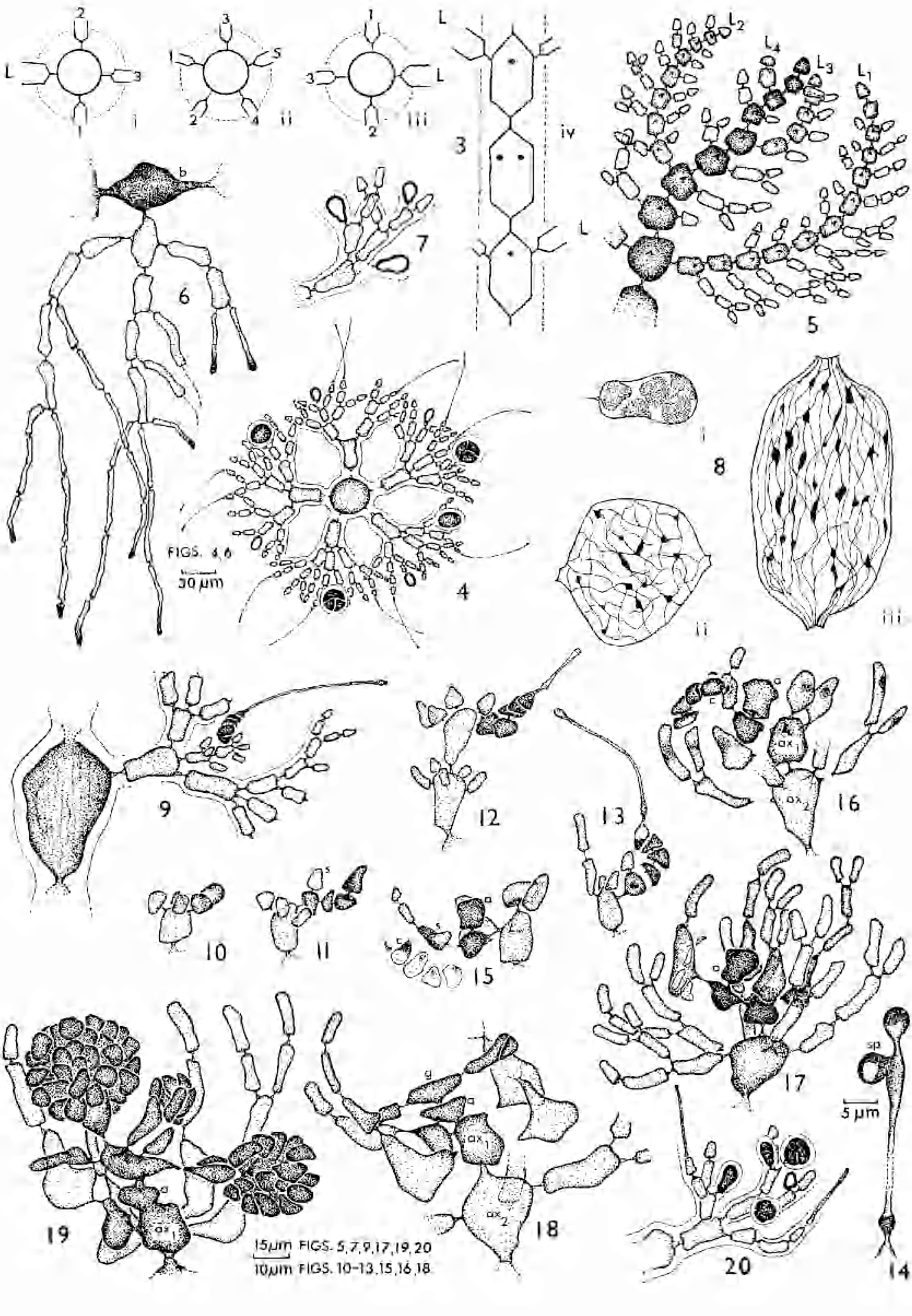
Fig. 16. Carpogonium (c) enlarged just prior to fusion with auxiliary cell (a); involucral filaments commencing to form from cells, including the supporting cell, of whorls on axial cells (ax_1, ax_2) of the fertile branch.

Fig. 17. Protrusion on auxiliary cell (a) marking position of fusion with connecting cell from carpogonium; small cell fragment remaining in place of carpogonium on degenerating carpogonial branch; marked increase in development of involucral filaments.

Fig. 18. Formation of pit-connection between lower part of auxiliary cell (a) and axial cell (ax_1) prior to breaking of connection between auxiliary cell and supporting cell; initials of 2 lateral groups of carposporangia formed on gonimoblast cell (g).

Fig. 19. Enlarged fusion between lower part of auxiliary cell (a) and axial cell (ax_1); succession of carposporangial groups forming on gonimoblast cell; supporting cell, free from carposporophyte, bearing involucral filament.

Fig. 20. Tetrasporangia and gland-cell borne in place of vegetative branches of whorl-branchlet.


FIGS. 4,6
30 µm
15µm FIGS. 5,7,9,17,19,20
10µm FIGS. 10–13,15,16,18
5 µm

the crystal-like inclusions recorded for these species. Branched cortical filaments bearing short outwardly-orientated chains of cells are similar to those found in *Ptilocladia pulchra* Sonder and a tendency towards distichous branching of the thallus, well defined in *Muellerena wattsii*, is also characteristic of the Crouanieae group and is best developed in species considered to be phylogenetically advanced.

Development of the procarp and carposporophyte also basically resembles that found in genera of Crouanieae. The 4-celled carpogonial branch is borne on a special fertile branch as in *Gulsonia*. The connecting cell involved in fusion between the carpogonium and auxiliary cell is much larger in *Muellerena wattsii* than in genera of Crouanieae, but subsequent development of the carposporophyte with lateral initiation of the two first-formed groups of carposporangia is similar to that seen in species of *Ptilocladia*, *Gulsonia* and *Euptilocladia* Wollaston. *Muellerena wattsii* differs, however, in elaboration of the involucre which surrounds the carposporophyte and in the secondary development of a pit-connection linking the lower part of the auxiliary cell to the axial cell upon which the procarp was developed. Following this fusion, the original connection between the supporting cell and the lower part of the auxiliary cell is usually broken so that the supporting cell functions as an enlarged basal cell of an involucral filament similar to its sister-cells of the whorl. The involucral filament borne on the supporting cell is initiated as a sterile cell on the supporting cell during enlargement of the carpogonial branch and elongates at about the same time as the other involucral branches commence to develop. These events probably allow a better nutritional supply to the carposporophyte while at the same time providing for development of the filamentous involucre. Although *Muellerena wattsii* differs from species of *Ptilocladia* in having a more consistent branching pattern, 5 whorl-branchlets per whorl, fusion between the auxiliary cell and fertile axial cell and a more elaborate involucre surrounding the carposporophyte, the two genera are basically similar in both vegetative and reproductive features. This similarity was noted by De Toni (1903) when he placed two species now recognised as *Ptilocladia pulchra* Sonder and *P. agardhiana* (Harvey) Woll. in the genus *Muellerena*. *M. wattsii* is also similar to *Gulsonia* in the presence of gland cells and the development of a special fertile branch bearing the procarp and, later, the carposporophyte. Thus it seems likely that *Ptilocladia*, *Gulsonia* and *Muellerena* are closely related and *Muellerena*, showing greater consistency in vegetative features and elaboration in carposporophyte organization, is phylogenetically the most highly advanced. The range of features already known for genera of the Crouanieae covers a possible evolutionary sequence leading to the increased organization and stability of thallus features characteristic of *Muellerena*. No similar relationship can be traced in the Dasyphileae or other group of the Ceramiaceae and it thus seems logical to include *Muellerena* in the tribe Crouanieae of the Ceramiaceae.

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